# Sexual Behavior

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## Abstract

Research on human sexual behavior is a multidisciplinary pursuit that seeks to understand one of the most vital and complex aspects of our biology. Foundations for this study include the basic principles of sexual selection, including differential reproductive roles of male and female, and the processes of sexual differentiation. Study of human sexual behavior is made vastly more complex by emotional involvements and the diversity of sexual behaviors exhibited by our species. Historically, sex researchers have struggled to overcome the methodological challenges involved with objective study of behavior in our own species and with the ethical and political implications of their work. Early research focused on merely quantifying the spectrum of human sexual behaviors and on understanding the physiological and psychological processes of sexual response. Subsequent work developed the concept of gender and began to address how behavioral and corporeal manifestations of sex can diverge from one another. Modern studies incorporate a variety of advanced scientific techniques to investigate mechanistic and functional hypotheses for specific behaviors. This review highlights four prominent research topics, highlighting current understanding, cutting edge work, and key issues for future research: mate preferences, concealed ovulation, sexual coercion, and homosexuality. In each of these areas of research, there is strong evidence for biological influences on behavior. It is also clear that known biological mechanisms only partly explain actual behavioral patterns, suggesting strong mediation by cultural, environmental, and developmental processes.

## INTRODUCTION

Sexual behavior is central to the biology of a species, being vital to how the species persists and changes over time. The study of sexual behavior in humans has produced particularly intense research effort, perhaps because of the unusual diversity of sexual behavior in our species and the central role sex plays in health, wellbeing, and popular culture. These factors magnify the complexity of gaining an objective understanding of sexual behavior in humans. Thus, at every stage in its history, scientific research on sex has been fraught with controversy for reasons ranging from inadequacy of sampling methods to ethical concerns to wider social implications. Sex research has

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both been shaped by and has steered social and political attitudes. As in any science, the field has built incrementally on its successes and failures, gradually incorporating new techniques and theoretical approaches. A field that began by simply attempting to catalog and describe the nature of sex in our species has moved forward into a vastly interdisciplinary research area incorporating advanced scientific methodologies such as genetics, neuroscience, and endocrinology, while acknowledging the complex interactions between culture, environment, experience, and biology in shaping behavior.

The study of human sexual behavior is prominently represented in several international research organizations, including the Society for the Scientific Study of Sexuality, the International Academy of Sex Research, the Society for Sex Therapy and Research, the Human Behavior and Evolution Society, and the American Sociological Association. In addition to targeted journals, such as the *Journal of Sex Research*, *Archives of Sexual Behavior*, and *Sex Roles*, research on sexual behavior figures prominently in broader journals in anthropology, psychology, sociology, and biology.

The following review provides a background to research in the field of sexual behavior, including historical perspectives, prominent approaches to modern studies of sex, and a highlight of four particularly active research areas. It should be noted that this is by no means an exhaustive treatment of sex research. Per the author's expertise, this review highlights research driven by or intersecting with a biological approach. For further discussion of related topics, refer to entries on gender in the Sociology series and on sex differences in behavior in the Anthropology series.

## FOUNDATIONS OF SEXUAL BEHAVIOR

### Sexual Selection

Foundations of sexual behavior in humans, as in other animals, stem from the core biological definition of male and female sex. Females are defined as the high-investment sex, demonstrated initially by a relatively large gamete (the ovum, or egg) containing the nourishment for early growth of the zygote. In mammals, where females bear the burden of pregnancy and lactation, the inequality in investment is particularly great. Thus, females and the investment they provide become a limiting resource for males who must compete for opportunities to fertilize them (Bateman, 1948). This has far-reaching implications for sexual behavior, as outlined in Darwin's presentation of sexual selection (Darwin, 1871) and its many subsequent elaborations. Males are generally expected to compete amongst themselves for access to females, a process that can shape behavior (e.g., aggression), morphology (e.g., body size, sexual ornaments), and physiology (e.g., sperm production). Males also

have the potential to produce offspring at a faster rate than females, often leading to relatively promiscuous mating behavior and a reluctance to invest too heavily in one mate when other opportunities are available. Females, on the other hand, are expected to be more conservative in their selection of mates, choosing males that are willing to provide an investment of resources or who have genetic traits that benefit offspring viability (Trivers, 1985). The difference in reproductive interests between the two sexes can create sexual conflict in which the strategies used by one sex cause negative effects for the other (Parker, 1979). Sexual coercion is a prominent outcome of sexual conflict in which males (typically) use force or the threat of force to circumvent female mate choice.

The above patterns are generalizations, and different species manifest them in different ways and to differing degrees. The human species presents a number of complications. Chiefly, the high cost of rearing human infants is thought to necessitate significant investment by fathers, often leading to long-term partnerships at the expense of mate-seeking behavior (Lancaster, J. B., & Lancaster, C. S., 1983). Whereas ostentatious displays and ornaments such as colorful feathers are more typical of males in other species, human females in most cultures use adornments to advertise beauty, youth, or fecundity to potential mates, suggesting that males' investment may compel them to be more selective. Humans display greater variability in sexual practices and more frequent nonconceptive sex than is typical of animals in nature. In addition, variation in cultural practices and the involvement of complex emotional and cognitive processes shape norms of sexual behavior.

## Sexual Differentiation

Biological research into human sexuality often references the developmental origins of male and female and persisting differences in the hormonal physiology of the two sexes. Initial sex determination is dependent on whether an individual receives an X (female) or a Y (male) chromosome from the father. The presence of a functional Y chromosome leads to maturation of the testes from an undifferentiated fetal gonad. Once the testes develop, they produce the hormone testosterone which, directly or indirectly, guides the maturation of the remainder of the male physical phenotype. Females' gonads and external genitalia derive from the same embryonic structures as males' in the absence of the Y chromosome and testosterone. This is an oversimplification of a process that, in fact, can be altered at various stages. The influence of these developmental processes on sexual behavior is far less clear-cut. Testosterone impacts male sexual behavior, as can be seen from the effects of castration in many species. However, it can have both "organizational"

effects, priming the neuroanatomical substrates at an early age of development, and "activational" effects, interacting with these substrates to produce behavioral responses in the mature organism. Testosterone may have important influences on the sexual behavior of females, as well, and it is known to have complex interactions with other hormones in both sexes. Females experience a cyclical fluctuation in the hormones progesterone and estradiol that accompanies the process of ovulation and menstruation. It is clear that sexual behavior in the human female is less strictly governed by these hormonal fluctuations than is the case for most other species.

## BRIEF HISTORY OF SEX RESEARCH

The modern study of human sexual behavior can be traced to Alfred Kinsey, founder of what is now the Kinsey Institute for Research in Sex, Gender, and Reproduction, and lead author of the Kinsey Reports on *Sexual Behavior in the Human Male* (Kinsey, Pomeroy, & Martin, 1948) and *Sexual Behavior in the Human Female* (Kinsey, Pomeroy, Martin, & Gebhard, 1953), among the first attempts to understand human sexual behavior from a scientific perspective. Kinsey's work was accomplished primarily through extensive interviews about sexual experiences and had the overarching goal of documenting the scope of human sexual behavior, as well as the frequency and sociocultural predictors of particular behaviors. Because his work emphasized the diversity of sexual experience, it was an important attempt to remove stigmas not only from the examination of sexual behavior but from the behaviors themselves. In particular, Kinsey documented the frequency of homosexual behavior, arguing that many individuals are not easily classified as either exclusively homosexual or exclusively heterosexual. While documenting differences in sexual drive between males and females, Kinsey reported a greater breadth and investment in sexual experience among women than was publicly recognized. These features made his research highly controversial at the time of publication. Though Kinsey's works are still highly regarded, they are criticized for methodological issues, such as reliance on self-reports, self-selection of individuals willing to discuss their experiences openly, and overrepresentation of gay subjects, sex workers, and sex offenders.

Beginning in the late 1950s, William Masters and Virginia Johnson extended the study of sexual behavior by documenting patterns of human sexual arousal and response (Masters & Johnson, 1966). In contrast to Kinsey's interview approach, Masters and Johnson conducted their research in a laboratory setting, monitoring physiological responses during masturbation or intercourse. Their work led to the recognition and description of the four phases of sexual response (excitement, plateau, orgasm, and resolution) and of multiple orgasmic potential in women. In addition, Masters and

Johnson targeted the assessment and treatment of sexual dysfunction, linking psychological and sexual health. However, by attempting to define "normal" versus "dysfunctional" behavior, their research moved away from Kinsey's emphasis on the diversity and individuality of sexual experience. This included their controversial treatment of homosexuality as a sexual dysfunction, one which they attempted to cure through conversion therapy. Such claims contributed to the maintenance of homosexuality in the American Psychiatric Association's *Diagnostic and Statistical Manual of Mental Disorders* until 1973.

After such intense scrutiny on the mechanics of sex, later attention focused on sexual identity. John Money redefined the term *gender*, and associated terms such as *gender role*, to highlight the distinction of biological sex from sex-typical behavior (Money & Ehrhardt, 1996). At the time, Money's view that gender was learned rather than innate was widely accepted, meeting agreement with a growing field of feminist scholarship that sought to reject ideas about the biological determination of gender roles. While Money's work was ground-breaking in highlighting the flexibility in behavioral manifestations of sex, he later earned fierce criticism because his recommendations led to a widespread and problematic medical practice of sexual reassignment for infants with ambiguous genitalia. Later gender scholars, to varying degrees, have acknowledged a more complex construction of gender, with influences of genes, hormones, environment, and developmental history. The development of gender identity and gender roles continues to be a major focal point of sex research.

## MODERN APPROACHES IN SEX RESEARCH

While early work in sex research relied primarily on narratives and on description and classification, the modern study of sexual behavior is truly interdisciplinary, cross-cutting many traditional fields and methodologies. Those with a biological leaning focus on understanding the diverse factors that predict variation in sexual behavior and reproductive patterns. This includes integration of data on genetics, hormone physiology, neurobiology, ecology, and demography. Those from a pure social science background explore the cultural contexts of sexual behavior and how sex shapes and is shaped by identity. These approaches meet in studies of sex from a public health perspective, where investigators study the risk factors and consequences for sexually-transmitted diseases, early/unwanted pregnancy, sexual violence, and other socially-relevant problems.

I highlight here several specific disciplines at the forefront of modern sex research:

- *Evolutionary psychology* seeks to understand how evolution has shaped the brain and behavior. Substantial constituents of this field focus on mate choice and the dynamics between mated partners. This field relies on the principle that, even in modern contexts, deep-rooted behavioral adaptations influence neuroanatomical structure and responses to everyday situations in ways that, accumulated over time, can positively impact fitness. These responses can be investigated by correlative studies or elicited in response to stimuli in experimental paradigms.
- *Biological anthropologists* also study sex within an adaptive framework, asking what characteristics of sexual behavior typify our species, how these characteristics differ from closely related species, through what evolutionary processes these features came about, how ecological context impacts the expression of sexual behavior, and how behavioral patterns affect reproductive success.
- *Developmental psychologists* study the impacts of biological mechanisms and rearing environments on the development of sexual behavior, particularly sexual orientation, gender identity, and sex differences. Much research focuses on transgendered individuals and those with intersex conditions.
- *Gender studies* scholars, variably represented in programs such as women's studies, sociocultural anthropology, gay/lesbian/bisexual/transgender studies, sociology, and visual and literary arts, focus on the cultural and biological contexts of gender, often with an eye towards the ethical and political landscape. While some gender scholars decry scientific approaches to gender, others interact closely with scientific literature to negotiate the cultural construction of biological processes.

## KEY QUESTIONS AND EMERGING TRENDS

### Mate Choice

A primary topic of study of sexual behavior in any species is partner choice. Following the predictions of sexual selection theory, females are predicted to be relatively choosy, given their limited reproductive opportunities, and to select features that reflect male genetic quality and/or willingness to invest resources in offspring. Males are predicted to be less choosy for sexual encounters, though perhaps more choosy in selection of a mate that will be invested in over a longer term. In choice of a long-term partner, males are expected to select signs of reproductive potential. Studies have generally borne out these predictions. Studies of mate choice have primarily been conducted in laboratory settings in which individuals are asked to rate attractiveness of subjects or make a forced choice. These studies

require careful design to assure that the variable of interest is isolated from competing stimuli. This may involve, for example, computer manipulation of images to alter specific facial features. Another common design assesses the attractiveness of odors by asking raters to smell t-shirts worn by another individual for several days under controlled conditions. Several consistent features of mate choice have been reported:

- *Fluctuating Asymmetry* (Gangestad, Thornhill, & Yeo, 1994). Asymmetries between the left and right halves of the body are generated by developmental instability, such as pathogen exposure. Both men and women find photographs and odors of people with low asymmetry to be more attractive.
- *Immunocompatibility* (Havlicek & Roberts, 2009). Women demonstrate a preference for the scents of partners with different profiles of the major histocompatibility complex (MHC), a set of genes that regulate immune response. By selecting partners with different MHC alleles from their own (or rare alleles), females maximize the ability of their offspring to respond to a variety of pathogens.
- *Sex-typical Features* (Geary, Vigil, & Byrd-Craven, 2004). Men's and women's faces show average differences in a number of key features as a result of differential exposure to sex hormones. Males are reported to find relatively feminized female faces (indicative of high estrogen levels) more attractive. Females find relatively masculine male faces most attractive, though this tendency varies with context. Women show correlated tendencies to prefer other masculine, testosterone-dependent features, such as deep voice, muscularity, and masculine displays. Men are reported to find a combination of relatively small waist and large hips most attractive in female partners.

Such studies have been criticized for focusing too closely on Western industrialized populations, and, in particular, on populations of college students who may not be behaving with marriage, or reproduction, in mind (Henrich, Heine, & Norenzayan, 2010). Certainly, the effect sizes of such studies are small, and the primacy of physical features over others (e.g., personality) has been exaggerated. However, it is important to note that the preferences outlined above have ample precedents in other species, thus their appearance in humans should not be surprising. Nevertheless, it is important to consider that humans experience substantial cultural differences in standards of beauty. Emerging research asks whether mate preferences exhibit cross-cultural variation, and if so, whether this can be attributed to differences in ecology or reproductive practices. For example, a study of Tanzanian hunter-gatherers found that the preference for symmetrical faces was even

more pronounced than in European cultures, perhaps because pathogen vulnerability is more ecologically relevant (Little, Apicella, & Marlowe, 2007).

Moving forward, research on mate choice needs to address two longstanding issues. First, mate preferences in experimental studies may not reflect actual choices given the availability of partners. Second, preferences for particular characteristics have been identified in isolation from others. Emerging research will assess how combinations of traits affect perceptions of attractiveness, the influence of individual rater characteristics on preferences, the comparability between preferences and realized mate characteristics, the consistency of characteristics across successive mates, and the effects of preferred versus nonpreferred characteristics on relationship quality. Important questions might include whether a disparity between preferred and actual mate characteristics leads to a shorter relationship, greater conflict, or a higher likelihood of infidelity. Longer term studies should address whether such choices have demonstrable effects on fitness. For example, recent evidence suggests that female body proportions preferred by males are associated with higher fecundity (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004).

### Concealed Ovulation

Many primates display prominent advertisements of ovulation, often accompanied by a behavioral "estrus", during which sexual behavior is enhanced. By contrast, humans lack such an obvious estrous display, and sexual behavior can occur at any time, lacking a strict reliance on hormones. This contrast generated a proliferation of arguments for the evolution of concealed ovulation in our species, many linking this phenomenon with the maintenance of long-term pair bonds and paternal effort. Subsequent scholars criticized that lack of visible estrus did not mean that ovulation was completely concealed and that "continuous" sexual receptivity did not preclude cyclic fluctuations in sexuality (Thornhill & Gangestad, 2008). Thus, emerging research addresses these issues:

- A large number of studies have examined frequency of sexual intercourse, masturbation, sexual fantasies, and sexual desire across the menstrual cycle. These studies provide frustratingly little consensus, perhaps because non-hormonal factors, such as daily experiences and relationship fluctuations, can have a strong impact. Some recent studies indicate that women may exhibit signs of enhanced receptivity, such as dressing more attractively or behaving more flirtatiously around the time of ovulation (Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007). Others, however, suggest that women may be more risk averse at ovulation (Chavanne & Gallup, 1998).

- Several lines of evidence suggest men have some ability to distinguish between women's preovulatory and postovulatory cycle phases, either through scent or in response to subtle changes in attractiveness (Haselton & Gildersleeve, 2011). Available data are not sufficient to suggest that men can pinpoint ovulation, that they consciously attempt to do so, nor that they can discern available cues outside of a controlled, experimental setting and in the absence of female behavioral cues. Newer research directions will focus more directly on these questions.
- A relatively new line of inquiry asks whether extended sexual receptivity coupled with subtle changes in attractiveness may allow women to pursue a mixed mating strategy. The hypothesis is that women face a tradeoff between two types of males, those that provide investment (likely to be long-term partners) and those that provide high quality genes (who may not be stable mates because of high appeal to other females). Extended receptivity allows women to pursue relationships with both types of males, while a subtle estrous period allows females to attract the highest quality male at the time of conception (Thornhill & Gangestad, 2008). Supporting evidence finds that women's preferences for particular male features (e.g., masculine features, symmetry) wax and wane across the cycle. This line of research is controversial, yet consistent with models from other pair-bonded species and with a low but non-negligible rate of cuckoldry in humans. This pattern sets up interesting lines of inquiry regarding sexual conflict. For example, men have been found to display increased mate guarding towards their partners near ovulation (Haselton & Gangestad, 2006).

The above research, dominated by scholars in evolutionary psychology, is both compelling in its bulk and controversial in its implications. Like studies of mate choice, far too many of these studies have relied on young, well-nourished Western samples and warrant replication in cross-cultural settings. Among the important considerations are that women in many traditional cultures, closer in lifestyle to our evolutionary past, spend the bulk of their lives pregnant and lactating. They experience very few ovulatory menstrual cycles and frequently conceive while still nursing their previous child, suggesting the existing literature could be unrepresentative of hormonal conditions in our evolutionary past (Lancaster & Kaplan, 2009).

### Sexual Coercion

Sexual coercion is a class of behaviors incorporating sexual harassment, domestic violence, rape, and other behaviors which forcibly limit female

behavior. These behaviors are of special importance and research difficulty because of their public health impacts. One body of research related to sexual coercion seeks to understand the extent of sexual violence and the personal and contextual risk factors that predict it. The Centers for Disease Control and World Health Organization have produced comprehensive reports on sexual violence in the United States and globally. Other researchers have produced survey results, primarily on college students (who are both common victims and perpetrators), in addition to analysis of attributes of convicted sex offenders. A second body of research acknowledges the pervasiveness of sexual violence across cultures, and thus seeks to understand the biological roots of the behavior. This line of research focuses on violence between intimate partners, comprising the majority of assaults. This approach is rooted in sexual conflict theory and uses models of sexual aggression in nonhuman species, including closely-related primates, in generating and testing hypotheses about human sexual violence (Muller & Wrangham, 2009). Both research directions must overcome considerable difficulties with reporting bias, as victims are less likely to report sexual violence than other types of crime, particularly in cases of acquaintance and spousal violence. Many recent studies rely on paired surveys of men and women and incorporate broader inquiries about sexual conflicts within relationships.

A recent work entitled *A Natural History of Rape* (Thornhill & Palmer, 2000) focused on the argument that human rape, like its analog in nonhuman species, is a behavioral adaptation by which men with limited sexual access attempt to gain fertilization opportunities. This text ignited considerable controversy both for its ethical implications and its tenuous empirical backing (Travis, 2003). However, it also generated renewed research interest in the topic. A more recent hypothesis poses that rape and other forms of sexual violence within relationships are tactics to protect the paternity certainty of the male partner (Goetz, Shackelford, Romero, Kaighobadi, & Miner, 2008). Similar punishment and intimidation tactics are utilized in the context of mate guarding among our closest primate relatives (Emery Thompson & Alvarado, 2012). A growing literature links intimate partner violence with suspicions of infidelity and the use of other types of possessive behaviors and suggest that predictors of rape are congruent with those for other forms of sexual violence within relationships. An important outcome of this work has been the push to recognize that biological underpinnings and proximate motivations are independent yet potentially complementary ways to explain such complex behaviors (Goetz *et al.*, 2008). The hope is that a better understanding of the evolutionary backdrop to sexual violence will aid in identifying individual and contextual risk factors.

### Homosexuality

While the early study of homosexual behavior fixated on questions of prevalence and normality, it has since become clear that forms of homosexual behavior are common in non-human species and across human cultures in widely varying environments. Emerging research has focused on discerning the biological factors affecting predispositions to homosexuality. Complementary work attempts to resolve how homosexual partnerships differ from those of heterosexual partnerships. These lines of research merge with a parallel literature on gender, attempting to identify correlations and divergence of gender identity with sexual orientation.

Several lines of evidence support biological predispositions to homosexuality:

- *Genetics*. Numerous studies report that close relatives of both male and female homosexuals have a higher likelihood of also being homosexual themselves (Bailey & Bell, 1993). Candidate genetic regions have been identified, including one on the X chromosome (Xq28 region) which may explain the high concordance of male homosexuality through the maternal line (Hu *et al*., 1995).
- *Intrauterine Effects*. Birth order is one of the strongest known predictors of male homosexuality, with the odds of homosexual identification increasing by 33% for each older brother a man has (Blanchard, 2004). It is hypothesized that this occurs because previous male fetuses prime mothers to produce a specific immune response to an antigen found on male cells (histocompatibility-Y, HY), leading to effects on brain development. M stress during gestation may have similar effects on neural development, though this hypothesis is yet not strongly supported. Specific effects that such fetal exposures may have on the brain are also unclear. Early work had pointed to a region of the hypothalamus, analogous to a part of the brain responsible for sexual behavior in other species, which was larger in heterosexual men than in women or homosexual men (LeVay & Hamer, 1994). This finding remains controversial.
- *Hormonal Effects*. A proliferation of studies have attempted to link prenatal androgen or estrogen exposure to homosexual behavior (Cohen-Bendahan, van de Beek, & Berenbaum, 2005). Many of these use sexually-dimorphic characteristics, such as digit length ratios, to estimate the uterine hormonal environment. These results do not reach a uniform conclusion, perhaps because these measures are too indirect. Other studies use individuals with known atypical hormonal environments and provide support that prenatal androgen exposure plays a contributing role in sexual orientation. Genetic males who are

insensitive to androgens adopt the typical sexual behavior of females. By contrast, genetic females with high uterine androgen exposure have a higher than average likelihood of becoming homosexual or bisexual (Meyer-Bahlburg, Dolezal, Baker, & New, 2008).

While there are compelling biological predictors of homosexuality, each single predictor explains only a fraction of the occurrence of homosexuality, suggesting that these factors each have only mild penetrance and/or that there may be large environmental influences. Curiously, there is little research to suggest which specific environmental features could play a role. Another flaw to this work is that it has primarily relied on self-identified homosexual orientation (yes or no), when such identification may be stigmatizing and when identification may not clearly be one or the other.

Some of the most intriguing new work focuses on the question of why, if homosexual behavior does not lead offspring production, it has persisted through evolutionary time. A prominent new hypothesis proposes that certain genes or processes that promote homosexual behavior also influence other traits that may, in fact, lead to high fitness outcomes. One replicated finding is that homosexual men have female maternal relatives with high fecundity (Camperio-Ciani, Corna, & Capiluppi, 2004). This suggests that such a gene is maintained by a process known as *sexually-antagonistic coevolution*, in which a gene that is evolutionary advantageous when expressed in one sex is disadvantageous in the other. An alternative, but not mutually-exclusive hypothesis, is that incomplete penetrance of a so-called "gay" gene could lead to high reproductive success. For example, psychologically masculine females or feminine men are less likely to identify as heterosexual than their peers, but when they do, have a higher than average number of sexual partners (Zietsch *et al*., 2008).

## CONCLUSION

The modern study of sexual behavior targets diverse aspects of sexuality, including partner preference, the dynamics between mated pairs, and the causes and consequences of nontraditional sexual behavior or gender identity. Cutting edge research is not merely descriptive but investigates the roles of biological and psychological mechanisms in shaping behavior, in addition to asking broader questions about the functions of the sexual behaviors observed in our species. Modern interdisciplinary perspectives are now better equipped to balance the biological and cultural aspects of sexuality and address the confluence of multiple developmental influences on behavior.

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